



## Increased mercury concentrations in walleye and yellow perch in lakes invaded by zebra mussels



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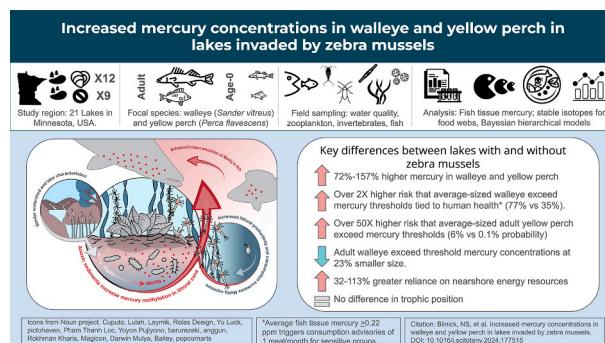
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### HIGHLIGHTS

- Invasive zebra mussels can alter mercury methylation and fish foraging in lakes.
- Fish tissue mercury was 72 %–157 % higher in lakes with zebra mussels.
- Over 2× risk that Hg in average-sized fish exceeds 0.22 ppm in zebra mussel lakes.
- Fish in lakes with zebra mussels rely more on littoral resources.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Zebra mussels (*Dreissena polymorpha*) are invasive species that alter ecosystems and food webs with the potential to affect aquatic mercury cycling and bioaccumulation in fishes, although the effect of zebra mussels on fish tissue mercury has not been tested in inland lakes. We assessed differences in fish tissue mercury concentrations and food webs in Minnesota lakes with and without zebra mussels while controlling for other lake and watershed characteristics. Mercury concentrations in adult walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) were 72 % and 157 % higher, respectively, in lakes containing zebra mussels compared to uninvaded lakes. Mercury in young of year (age-0) fish was also elevated, with mercury concentrations 97 % and 82 % higher in age-0 walleye and yellow perch, respectively, in zebra mussel lakes. Walleye mercury concentrations exceeded 0.22 ppm — a threshold triggering more restrictive human consumption advisories for sensitive populations — at a 23 % smaller size, and average-sized walleye (420 mm) exceeded this threshold at a rate of 77 % in invaded lakes,

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compared to 35 % in uninvaded lakes. Walleye and yellow perch relied more on littoral resources in lakes with zebra mussels but did not feed at meaningfully higher trophic levels. Increased fish tissue mercury in lakes invaded by zebra mussels have consequential implications for fisheries and human health.

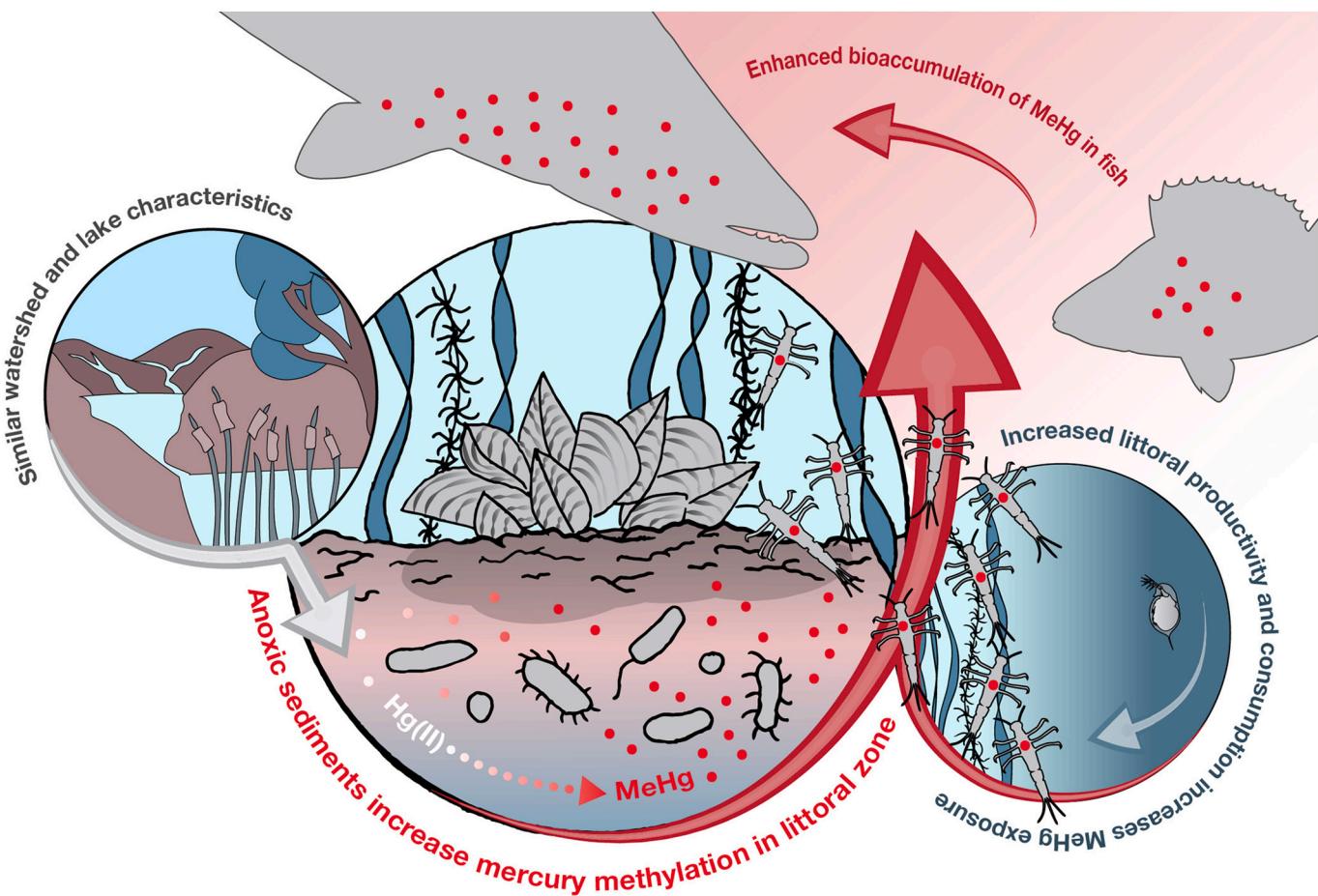
## 1. Introduction

Mercury contamination of aquatic ecosystems is a substantial public health issue, and mercury is responsible for about 80 % of all fish consumption advisories globally (Eagles-Smith et al., 2018). Managing aquatic ecosystems to limit mercury exposure requires an understanding of global-to-local factors that influence mercury loading, cycling, and uptake by organisms (Driscoll et al., 2013; Krabbenhoft and Sunderland, 2013; Eagles-Smith et al., 2018). In aquatic ecosystems, mercury is converted to the bioavailable and neurotoxic form, methylmercury, by microorganisms (Gilmour et al., 1992), and this process is affected by multiple chemical, physical, and biological variables (Morel et al., 1998; Ullrich et al., 2001; Bravo and Cosio, 2020). The biomagnification of methylmercury within aquatic food webs has caused fish consumption advisories across the Great Lakes region (Evers et al., 2011). Mercury concentrations in piscivorous fish in many inland lakes in the upper Midwestern United States have increased in recent decades despite declining atmospheric deposition of mercury (Rasmussen et al., 2007; Monson, 2009; Monson et al., 2011), and the causes of these increasing

trends are largely unknown.

Mercury bioaccumulation in fish can be affected by the amount of methylmercury produced in the aquatic environment, and also by fish growth rates, diets, and food web dynamics (Kidd et al., 2011; Eagles-Smith et al., 2018; Kozak et al., 2021). Aquatic invasive species can alter food webs and increase contaminant bioaccumulation in fishes by increasing reliance on littoral vs. pelagic prey resources (Eagles-Smith et al., 2008; Azim et al., 2011) and/or increasing trophic position (Vander Zanden and Rasmussen, 1996; Rennie et al., 2011). However, responses of fish tissue mercury to species invasions are mixed due to multiple competing pathways through which aquatic invasive species affect food webs, and fish growth, and resource use (e.g., Swanson et al., 2003; Prestie et al., 2019; Rennie et al., 2024). Considering the complex processes driving methylmercury formation and bioaccumulation in fishes together with the multiple pathways through which species invasions alter aquatic ecosystems and food webs, predicting the overall effects of aquatic species introductions on mercury concentrations in fish is not straightforward.

Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena*



**Fig. 1.** Conceptual figure illustrating the hypothesized pathways through which zebra mussels influence lake food webs and mercury methylation. Mercury in sediments is influenced by watershed characteristics and water quality conditions, which did not differ between invaded and uninvaded lakes. Zebra mussels can cause anoxia in nearshore sediments, potentially increasing mercury methylation in the littoral zone. At the same time, zebra mussels shunt nutrients from the open water pelagic zone to the nearshore littoral zone, increasing littoral production. If fish in invaded lakes rely more heavily on littoral energy sources, the combined effects of increased littoral production and increased mercury methylation in nearshore zones could lead to increased mercury concentrations in fish in lakes containing zebra mussels compared to uninvaded lakes.

*bugensis*; collectively dreissenids) are filter-feeding bivalves that are invasive in North America. Dreissenids alter aquatic ecosystems through multiple pathways (Higgins and Vander Zanden, 2010; Karatayev and Burlakova, 2022), with the potential to alter the mercury cycle in at least two ways: (1) physicochemical changes to the nearshore environment impacting mercury methylation, and (2) alteration of food web structure changing mercury bioaccumulation in fishes (Fig. 1). Dreissenid mussels form dense mats that can result in anaerobic sediments (Higgins and Vander Zanden, 2010; Zaiko et al., 2010), which in turn creates conditions more favorable for mercury methylation by obligate anaerobic microbial communities (Bravo and Cosio, 2020). At the same time, zebra mussels increase water clarity (Macisaac, 1996), promoting photodemethylation (a net loss of aqueous methylmercury) in the photic zone prior to bioaccumulation (Lehnher and St., 2009). Furthermore, dreissenids alter energy cycling of invaded lakes. Dreissenids filter nutrients from open water and expel them on the lake bottom as waste products, simultaneously reducing pelagic and increasing benthic energy production (e.g., Stewart et al., 1998; Hecky et al., 2004; Gergs et al., 2009; Mayer et al., 2013) and increasing the availability of benthic prey resources (e.g., Ward and Ricciardi, 2007; Higgins and Vander Zanden, 2010; Ozersky et al., 2012). As a result, fish may change their feeding habits to rely more on littoral resources (Rennie et al., 2013; Turschak et al., 2014; Fera et al., 2017; Morrison et al., 2021). Collectively, these changes have major implications for aquatic mercury cycling and bioaccumulation in fish, as zebra mussels simultaneously create biogeochemical conditions promoting greater methylmercury production in the littoral zone while concentrating energy production and fish consumption of prey in these areas (Fig. 1; Lepak et al., 2019). Indeed, dreissenid mussel invasions were associated with increased mercury concentrations in fish tissues in Lake Michigan despite ongoing reductions in mercury emissions in the airshed (Azim et al., 2011; Lepak et al., 2015, 2019). However, due to a lack of studies on the effects of zebra mussels on mercury cycling in small inland lakes, it is unknown whether ecosystem changes associated with zebra mussels results in altered fish tissue mercury concentrations in inland lakes that currently support high levels of fish harvest for human consumption.

Here, we examine the effects of invasive zebra mussels on fish tissue mercury and food webs in Minnesota lakes. We sampled lakes with and without zebra mussels with comparable water quality and watershed characteristics known to affect mercury loading, methylation, and bioaccumulation. We focus on walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*), two culturally, economically, and ecologically important freshwater fish species (Riener, 2004; Feiner and Höök, 2015) that are frequently consumed by Indigenous communities and recreational anglers (Kappen et al., 2012; Schroeder and Fulton, 2013). Both species are zooplanktivorous in early life, while as adults walleye are primarily piscivorous and yellow perch are primarily invertivorous (Mittelbach and Persson, 1998; Graeb et al., 2005). Yellow perch are consumed by walleye and other piscivores, and mercury concentrations in predators and prey from the same lake may be correlated due to both direct consumption and to shared responses to their environments (e.g., Wiener et al., 1990; Sumner et al., 2020). Both species demonstrate flexibility in pelagic vs. littoral resource reliance (Stasko et al., 2015; Tunney et al., 2018) so have the capacity to take advantage of increased littoral resources in response to food web and habitat changes caused by zebra mussel invasion. We predicted that walleye and yellow perch from lakes containing zebra mussels would have higher mercury concentrations and rely more heavily on littoral resources compared to uninvaded lakes.

## 2. Materials and methods

### 2.1. Study lakes

We sampled 21 lakes (105–4051 ha) in Minnesota; 12 containing zebra mussels and 9 without (Fig. S1). We prioritized lakes with active

management of walleye scheduled for standard fish monitoring surveys to supplement our data collection. We selected lakes with similar morphometric and watershed characteristics to control for factors unrelated to zebra mussels that may contribute to differences in fish tissue mercury (Table S1). Lakes were assessed for dissolved organic carbon (DOC), particulate total Hg, filtered total Hg, particulate MeHg, and filtered MeHg to determine if there were substantial differences in aqueous Hg concentrations that could drive differences in fish tissue Hg between lakes with and without zebra mussels. DOC was also analyzed due to the close connection between Hg and carbon cycling in many environments (e.g., Lavoie et al., 2013; Janssen et al., 2024). Water samples were collected from shore from all lakes from October to November 2021 using trace metal clean techniques (Olson and DeWild, 1999). Raw water was filtered using quartz fiber filters (0.7 µm pore size) then samples for filtered Hg analysis were preserved with 1 % hydrochloric acid and filters were frozen until analysis. Samples for dissolved organic carbon (DOC) analysis were refrigerated until analysis and stored no longer than two weeks. Secchi depth and water temperature were measured at the time of organismsampling.

Water samples were analyzed using standard U.S. Environmental Protection Agency methods for total mercury (United States Environmental Protection Agency, 2002), methylmercury (United States Environmental Protection Agency, 2001), and DOC (Potter and Wimsatt, 2005). Water replicates were collected from five sites for quality assurance, the average relative percent difference was 1 % (0–2 % range) for DOC, 8 % (3–12 % range) for filtered THg, 7 % (0–20 % range) for particulate THg, and 5 % (0–13 % range) for particulate MeHg. Only two samples were above the method detection limit (0.04 ng L<sup>-1</sup>) for filtered MeHg (Table S1). Field and laboratory blanks had no detectable THg (<0.05 ng L<sup>-1</sup>) or DOC (<0.10 mg L<sup>-1</sup>). All analyses met the quality control and assurance guidelines set forth by the USGS Mercury Research Lab (MRL) and all raw THg, MeHg, and DOC data are available within the companion USGS data release (Tate et al., 2022).

To assess whether lake and watershed characteristics differed among invaded and uninvaded lakes, we collated data on lake morphometry (lake area, lake volume, proportion littoral area defined as area under 4.5 m depth, and maximum depth), watershed area, and area of wetlands and agricultural land use (defined as cultivated plus pasture area) in the watershed from state agency databases (<https://gisdata.mn.gov/>) and extracted lake hydrologic connectivity from the LAGOS-US database (Cheruvelil et al., 2021). We compared water quality measurements and lake and watershed characteristics among invaded and uninvaded lakes using non-parametric Wilcoxon tests (Wilcoxon, 1945), with a null hypothesis that lakes from uninvaded and invaded lakes came from the same population of lakes.

### 2.2. Organism collection

Lakes were sampled in 2019, 2020, or 2021. Fish and invertebrates were collected within a 1–4 week period from each lake primarily in summer months, with some supplementary fish collected in October to bolster sample sizes for difficult to sample groups (Table S2). We sampled walleye and yellow perch as both age-0 and subadult/adult fish from each study lake to reflect ontogenetic diet shifts (Table S3, Table S4). Age-0 fish were collected with beach seines, nighttime electrofishing, and/or monofilament micromesh gillnets (Boehm et al., 2020). Age-0 walleye were difficult to collect from many study lakes, necessitating fall electrofishing collections from many lakes to ensure representation in our sample (Table S2). Fish were humanely euthanized using a lethal dose of MS-222 (Leary et al., 2020). Adult and sub adult (>age-0; hereafter “adult”) walleye and yellow perch were obtained from standard monitoring surveys conducted by the Minnesota Department of Natural Resources (MNDNR) using gillnets and trapnets set for approximately 24 h at index stations throughout the lakes (Minnesota Department of Natural Resources, 2017). To account for spatial variability within each lake, each specimen type was collected at

3–6 sites per lake. Fish were placed in a cooler with dry ice and kept frozen until dissected. Fish tissue samples consisted of white dorsal muscle above the lateral line, which were rinsed in deionized water prior to drying. For small age-0 fish (individuals <5 cm), the guts, heads, and tails were removed, and the rest of the body was used. Each fish sample consisted of tissue from a single individual. Pelagic zooplankton were collected with a simple plankton net (30-cm diameter opening, 80  $\mu$ m mesh) via vertical tows at 3–5 sites per lake at the deepest points, or 30 m if the lake exceeded that depth (range: 4–30 m). Zooplankton samples were preserved immediately in undiluted reagent-grade 90.5 % ethanol and further sorted by hand under a microscope to select copepods and cladocerans. Profundal zebra mussels were collected with a Ponar grab at ~12 m depth, or at depths close to the maximum depth of the lake if it was <12 m (range: 3.9–13.2 m). Littoral invertebrates - mainly Amphipoda, Gastropoda, and Ephemeroptera - were collected at 0–1.5 m of depth with kick nets, and native mussels and snails were collected using kick nets or snorkeling. Specimens were initially stored in vials of cool lake water and allowed several hours to evacuate their gut contents before being sorted and pooled based on family and functional feeding group (Merritt and Cummins, 1996) and frozen for later analysis. Gastropods and unionid mussels muscle tissue was removed from the shells and frozen.

### 2.3. Fish tissue mercury analysis

A subsample of individual fish that were analyzed for C/N stable isotopes were sent for additional total mercury analysis (Table S5). Subsamples of dorsal muscle tissue were analyzed for total mercury following established protocols (United States Environmental Protection Agency, 1998). Total mercury concentrations in fish dorsal muscle tissues were used as a proxy for methylmercury, because >95 % of total mercury in fish tissues is methylmercury (Bloom, 1992). Fish tissue mercury was measured by the USGS MRL in Madison, WI, via combustion coupled to atomic absorption spectroscopy (United States Environmental Protection Agency, 1998) with a Nippon Instrument Corporation (NIC) MA-3000 (direct mercury analyzer). Certified reference material (International Atomic Energy Agency [IAEA] 407) was analyzed every 10 samples to determine accuracy and precision of measurements and showed acceptable recoveries ( $227.5 \pm 13.8 \text{ ng g}^{-1}$ ,  $97 \pm 15 \text{ % recovery}$ , 1SD,  $n = 98$ ). Tissue for mercury analysis was weighed before and after drying (at 60 °C for 24–48 h) to allow for back calculation of water content for reporting mercury concentrations as wet weights (mean $\pm$ SD proportion water of adult walleye =  $0.80 \pm 0.02$ ; adult yellow perch =  $0.80 \pm 0.03$ ; age-0 walleye =  $0.81 \pm 0.01$ , age-0 yellow perch =  $0.78 \pm 0.05$ ). The raw concentration data (THg) was converted from ng/g (dry weight) to ppm (wet weight) for comparison with state fish tissue consumption advisory standards using Eqs. (1) & (2):

$$\text{fraction of water content} = (\text{wet weight(g)} - \text{dry weight(g)}) / \text{wet weight (g)} \quad (1)$$

$$\text{Hg ppm} = \text{Hg ppm (dry weight)} \times (1 - \text{fraction of water content}) \quad (2)$$

All mercury concentration data are in the corresponding USGS data release (Tate et al., 2022).

We assessed differences in total mercury in fish tissues between invaded and uninvaded lakes using Bayesian hierarchical models in the 'brms' package (Bürkner, 2021) in R (R Core Team, 2023). We used diffuse priors from a Gaussian distribution and included four chains of 2000 iterations with a burn in of 1000 and thinning rate of 1. Gelman and Rubin tests and visual inspection of trace plots confirmed model convergence (Rhat values  $\leq 1.01$ ). Fixed effects included fish total length (scaled within each fish grouping using z-scores), invasion status of the lake, species/age grouping, an interaction between invasion status and species grouping, and an interaction between fish length and mercury

concentration to allow that relationship to vary among species. We also included as fixed effects lake-level covariates known to affect mercury cycling (lake area, lake to watershed area ratio, percent wetlands in the watershed, and lake hydrologic connectivity). These covariates were chosen based on past research showing correlations with mercury in aquatic systems (Bodaly et al., 1993; Rasmussen et al., 2007; Hutcheson et al., 2008; Rypel, 2010) and data availability. Model structure is shown in Eq. (3):

$$\begin{aligned} \log(Y_{ij}) | b_j &\sim \text{Gaussian}(\mu_{ij}, \sigma^2) \\ \mu_{ij} &= \beta_0 + b_j + \beta_1 \text{scaled.length}_{ij} + \beta_2 I(\text{species}_i \\ &= \text{Age0YellowPerch}) + \beta_3 I(\text{species}_i = \text{AdultWalleye}) + \beta_4 I(\text{species}_i \\ &= \text{Age0Walleye}) + \beta_5 I(\text{invasion}_j \\ &= \text{ZM}) + \beta_6 \text{scaled.lake.percent.wetland}_j + \beta_7 \text{scaled.log.watershed} \\ &: \text{lake.area}_j + \beta_8 \text{scaled.log.lake.area}_j + \beta_9 I(\text{hydrologic.class}_j \\ &= \text{DrainageLk}) + \beta_{10} I(\text{hydrologic.class}_j \\ &= \text{Isolated}) + \beta_{11} \text{scaled.length}_{ij} * I(\text{species}_i \\ &= \text{Age0YellowPerch}) + \beta_{12} \text{scaled.length}_{ij} * I(\text{species}_i \\ &= \text{AdultWalleye}) + \beta_{13} \text{scaled.length}_{ij} * I(\text{species}_i \\ &= \text{Age0Walleye}) + \beta_{14} I(\text{species}_i = \text{Age0 Yellow Perch}) * I(\text{invasion}_j \\ &= \text{ZM}) + \beta_{15} I(\text{species}_i = \text{Adult Walleye}) * I(\text{invasion}_j \\ &= \text{ZM}) + \beta_{16} I(\text{species}_i = \text{Age0 Walleye}) * I(\text{invasion}_j = \text{ZM}) \end{aligned} \quad (3)$$

$$b_j \sim N(0, \sigma_b^2)$$

where  $Y_{ij}$  = mercury concentration for fish  $i$ , sampled from lake  $j$ .  $\beta_0$  is the overall intercept and includes adult yellow perch, uninvaded lakes, and drainage as the reference conditions.  $\beta_1$  is the estimated effect of fish length, while  $\beta_{11}$ – $\beta_{13}$  are the interactive effects that allow that relationship to vary by species.  $\beta_2$ – $\beta_4$  are the estimated effects of each taxonomic group (estimated as the difference from the adult yellow perch reference condition),  $\beta_5$  is the estimated effect of zebra mussel invasion (estimated as the difference from the uninvaded reference condition), and  $\beta_7$ – $\beta_8$  are the estimated interactive effects of zebra mussel invasion and taxonomic group that allows the estimated effect of zebra mussel invasion to vary among taxa. For all effects of categorical variables,  $I$  is an indicator variable set to 1 when the condition is true and 0 otherwise.  $\beta_6$ – $\beta_{10}$  are estimated effects of lake area, lake to watershed area ratio, and percent wetlands, and additional terms for categorical lake connectivity classes (isolated = no surface water inputs or outputs; drainage = surface water inlets and outlets; drainage lake = surface water inlets and outlets with at least one upstream lake >10 ha) accessed from the LAGOS-US database (Smith et al., 2021). Lake-level intercepts ( $b_j$ ) were included as a random factor. Model code and data are available (Blinick et al., 2023). We also fit a model without lake level covariates to test the influence of these variables on our conclusions.

### 2.4. Food web analysis

We used stable isotope analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Vander Zanden and Rasmussen, 1999; Post, 2002) to quantify littoral reliance and trophic position of walleye and yellow perch. Tissue samples for stable isotope analysis were collected from pelagic zooplankton, littoral and profundal invertebrates, and walleye and yellow perch primarily in June–August (Table S2). All fish, macroinvertebrate, and zooplankton samples were dried at 60 °C for 24–48 h, ground to a powder, and ~1 mg subsamples were packed in tin capsules. Tissue samples were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  by the University of California-Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Analytical precision (standard deviation) was between  $\pm 0.04$ – $0.17$  % for  $\delta^{13}\text{C}$  and  $\pm 0.06$ – $0.10$  % for  $\delta^{15}\text{N}$ . Final delta values were reported as ratios of  $^{13}\text{C}^{12}\text{C}$  and  $^{15}\text{N}^{14}\text{N}$  relative to international standards Vienna PeeDee Belemnite and Air for C and N, respectively. Because preservation in ethanol can influence zooplankton stable isotope composition (Sarakinos et al., 2002; Feuchtmayr and Grey, 2003), we applied an ethanol correction factor based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of paired samples of frozen and preserved zooplankton (Blechinger et al., 2024).

Consumer reliance on littoral resources were determined using  $\delta^{13}\text{C}$  values of fish relative to baseline  $\delta^{13}\text{C}$  of primary consumers from littoral and pelagic areas (Fig. S2). Although fish do not consume the baseline food sources directly, relatively long-lived primary consumers provide representative signals of basal littoral and pelagic  $\delta^{13}\text{C}$  source (Vander Zanden and Rasmussen, 1999; Post, 2002). We estimated dietary contributions of littoral resources for each fish grouping using Bayesian isotopic mixing models in the R package MixSIAR (Semmens et al., 2009; Stock et al., 2018). To correct for trophic discrimination,  $\delta^{13}\text{C}$  of each fish were adjusted such that  $\delta^{13}\text{C}_{\text{TEF}} = \delta^{13}\text{C}_{\text{fish}} - \Delta$ , where  $\Delta$  is described in Eq. (1) following Turschak et al. (2019):

$$\Delta = \text{TEF}_C [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{PC}}) / \text{TEF}_N] \quad (4)$$

The trophic enrichment factors account for the average shift per mil in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from fractionation that occurs from one trophic level to another ( $\text{TEF}_C = 0.39$  ‰ and  $\text{TEF}_N = 3.4$  ‰, Post, 2002).  $\delta^{15}\text{N}_{\text{PC}}$  represents the overall primary consumer baseline of  $\delta^{15}\text{N}$ , calculated as the mean  $\delta^{15}\text{N}$  value for all littoral and pelagic primary consumers in each lake. Following Silberberger et al. (2021) we elected not to lipid correct isotope values outside of the ethanol correction described in (Blechinger et al., 2024) to avoid introducing additional uncertainty, as many of our invertebrate C:N ratios fell far outside the range of the data used to develop the equation that is typically used for aquatic organisms (Post et al., 2007). Separate MixSIAR models were fit for each species-age group with a random intercept for lake and fixed effects of invasion status. Each model was run using uniform priors with a multiplicative residual and process error structure. The models were fit using 3 Markov chains with 3,000,000 iterations, a 1,500,000 iteration burn-in, and a 500 thinning rate. Model convergence was confirmed based on Gelman-Rubin R-hat values  $<1.01$  and that  $<5$  % of Geweke z scores were outside of the 95 % CI.

Trophic position of each fish was estimated following Rybczynski et al. (2008).

$$TP = \left[ \frac{\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{PC}}}{\text{TEF}_N} \right] + 2 \quad (5)$$

where  $\delta^{15}\text{N}_{\text{fish}}$  is each individual  $\delta^{15}\text{N}$  value,  $\delta^{15}\text{N}_{\text{PC}}$  represents the overall primary consumer baseline of  $\delta^{15}\text{N}$  (calculated as the mean  $\delta^{15}\text{N}$  value for all littoral and pelagic primary consumers in each lake), and  $\text{TEF}_N = 3.4$  ‰ (Post, 2002). Trophic position was calculated assuming primary consumers ( $TP = 2$ ) were one trophic position above the base of the food web.

We assessed differences in trophic position between invaded and uninvaded lakes using Bayesian hierarchical models in the `brms` package (Bürkner, 2021) in R (R Core Team, 2023). We used diffuse priors from a Gaussian distribution. Model structure was similar to Eq. (3), where  $Y_{ij}$  = the trophic position for fish  $i$ , and lake  $j$ . In this case we did not include lake-level covariates or interactive effects of species and fish total length.

### 3. Results

#### 3.1. Fish tissue mercury concentrations

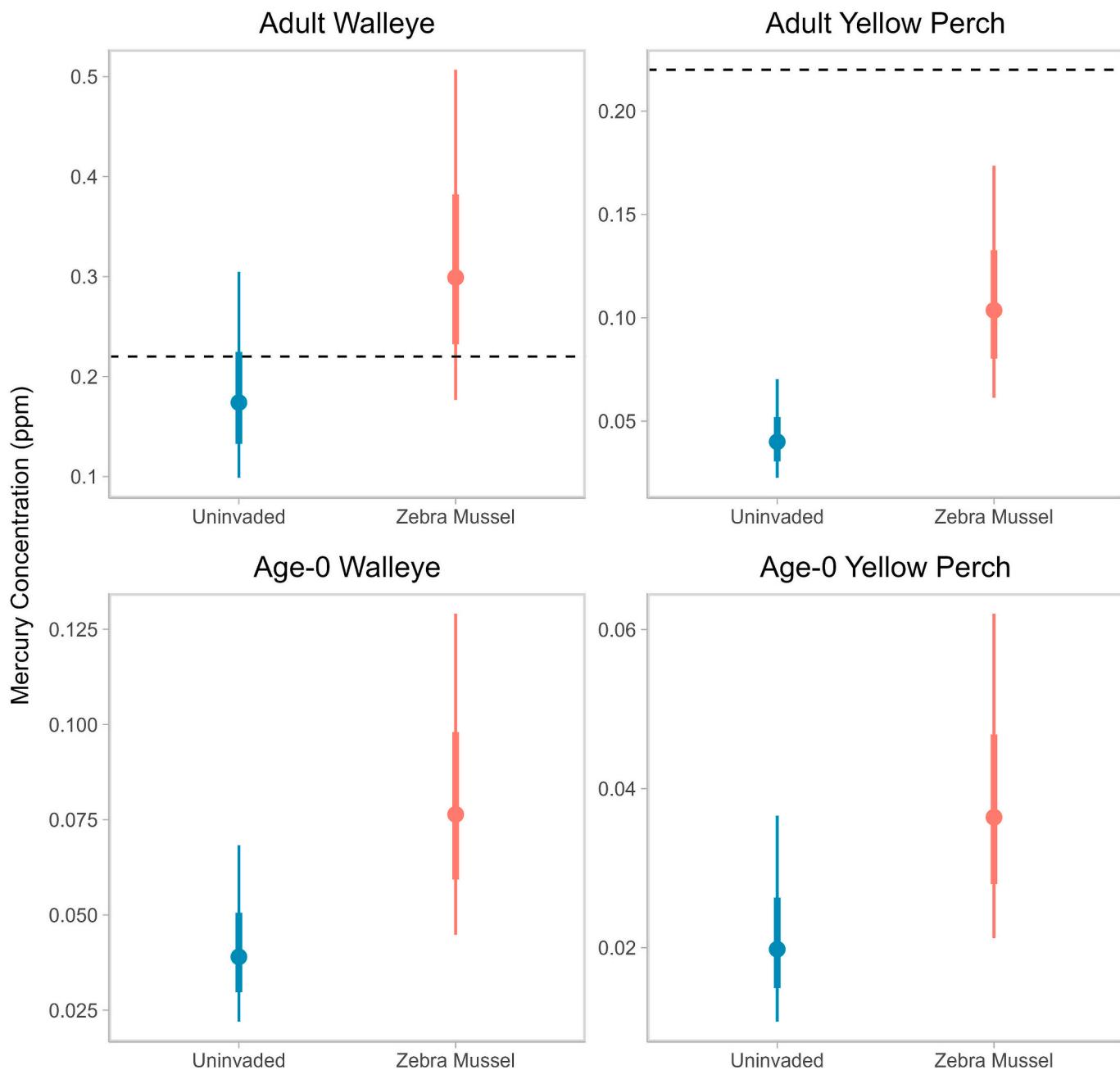
Mercury concentrations were higher in fish of all life stages from lakes containing zebra mussels compared to uninvaded lakes (Fig. 2), although 95 % credible intervals of the difference between mercury

concentrations for a fish of average size included zero in all cases except for adult yellow perch (Table S6). Total mercury concentrations in fish tissue were 72 % (95 % CI:  $-24$  %– $289$  %) higher for adult walleye and 157 % (95 % CI:  $14$  %– $495$  %) higher for adult yellow perch in lakes containing zebra mussels compared to uninvaded lakes (Fig. 2, Table S6). Median mercury concentration in adult walleye of average size (419 mm or 16.5 in) from lakes with zebra mussels was 0.30 ppm (95 % CI:  $0.18$ – $0.51$ ), 1.4 times greater than the 0.22 ppm threshold that warrants reducing the frequency of fish consumption from one meal/week to one meal/month for sensitive groups (Great Lakes Consortium, 2007) and 1.7 times higher than the median concentration in walleye of the same size from an uninvaded lake of 0.17 ppm (95 % CI:  $0.01$ – $0.31$ ). Mercury concentrations in fish varied among lakes (Fig. S3). In 9 of 12 invaded lakes, median mercury concentrations in adult walleye of average length exceeded 0.22 ppm, while in uninvaded lakes median estimated concentrations exceeded 0.22 ppm in 3 of 9 lakes. Age-0 fish exhibited similar patterns (Fig. 2), mercury concentrations in age-0 fish were 97 % (95 % CI:  $-16$  %– $357$  %) higher for walleye and 82 % (95 % CI:  $-23$  %– $338$  %) higher for yellow perch in lakes containing zebra mussels (Table S6).

Mercury concentrations increased with increasing fish total length (Fig. 3). Median mercury concentrations in adult walleye were predicted to exceed 0.22 ppm at lengths  $> 352$  mm (13.9 in) in zebra mussel-invaded lakes, compared to 456 mm (18.0 in) in uninvaded lakes (Fig. 3). Adult walleye of average size (419 mm or 16.5 in) were more than twice as likely to exceed this threshold in lakes with zebra mussels (probability = 0.77) compared to uninvaded lakes (probability = 0.35; Fig. S4). Median mercury concentrations in adult yellow perch were predicted to exceed the 0.22 ppm threshold at lengths  $> 224$  mm (8.8 in) in lakes with zebra mussels, and were never predicted to exceed 0.22 ppm in uninvaded lakes (Fig. 3). Adult yellow perch of average size were  $>50$  times more likely to exceed 0.22 ppm of mercury in lakes with zebra mussels (probability = 0.06) compared to uninvaded lakes where this probability was near zero (probability = 0.001). The relationship between fish length and mercury concentration varied by species (Table S7). Estimated coefficients for all other lake-level covariates suggest that mercury concentrations were higher in drainage lakes and in lakes with large watershed to lake area ratios, although parameter estimates for lake level covariates were not statistically distinguishable from zero (Table S7).

#### 3.2. Food web comparison

Walleye and yellow perch relied on average more on littoral energy resources in lakes with zebra mussels than in uninvaded lakes (Fig. 4), although the 95 % credible interval of the difference between invaded and uninvaded lakes overlapped 0 for all species groups except adult walleye (Table S8). In lakes containing zebra mussels, littoral reliance was 32 to 113 % higher than in uninvaded lakes, with high uncertainty in estimates for all groups (Table S8). Adult yellow perch exhibited the greatest difference in proportional littoral reliance between invaded and uninvaded lakes (0.21 or 113 % increase; 95 % CI:  $-0.08$ – $0.46$  ppm), and age-0 walleye exhibited the smallest difference (0.16 or 32 % increase; 95 % CI:  $-0.18$ – $0.44$  ppm). Trophic positions of walleye and yellow perch did not differ as a result of zebra mussel invasion status in our study, although the trophic position of walleye was greater than that of yellow perch for both age groups (Table S9) and increased with increasing fish length (Table S10). Trophic position of adult walleye, adult yellow perch, and age-0 walleye from lakes with zebra mussels were slightly elevated relative to that of uninvaded lakes, but the magnitude of these differences was small in biological terms (difference of  $-0.03$  to  $0.24$  trophic levels, or  $-1$  % to  $7$  % percent change) and 95 % credible intervals of differences overlap zero for all groups (Table S9). Lake-specific estimates of littoral reliance and trophic position are presented in Fig. S5.



**Fig. 2.** Mercury concentrations of adult and age-0 walleye and yellow perch in lakes invaded by zebra mussels and uninvaded lakes. Mercury concentrations (in ppm wet weight) represent model-estimated concentrations for fish of mean total length for each group (adult walleye 420 mm or 16.5 in; adult yellow perch 151 mm or 6.0 in; age-0 walleye 142 mm or 5.6 in; age-0 yellow perch 51 mm or 2.0 in) and at average conditions of other covariates (estimates are averaged across all levels of lake connectivity class). Dots represent medians; heavy lines represent 66 % credible intervals, and thin lines represent 95 % credible intervals of expected values for each group from an average lake. The horizontal dotted lines at 0.22 ppm represent the Minnesota Department of Health (Great Lakes Consortium, 2007) threshold that warrants reducing the frequency of fish consumption from one meal/week to one meal/month for sensitive groups.

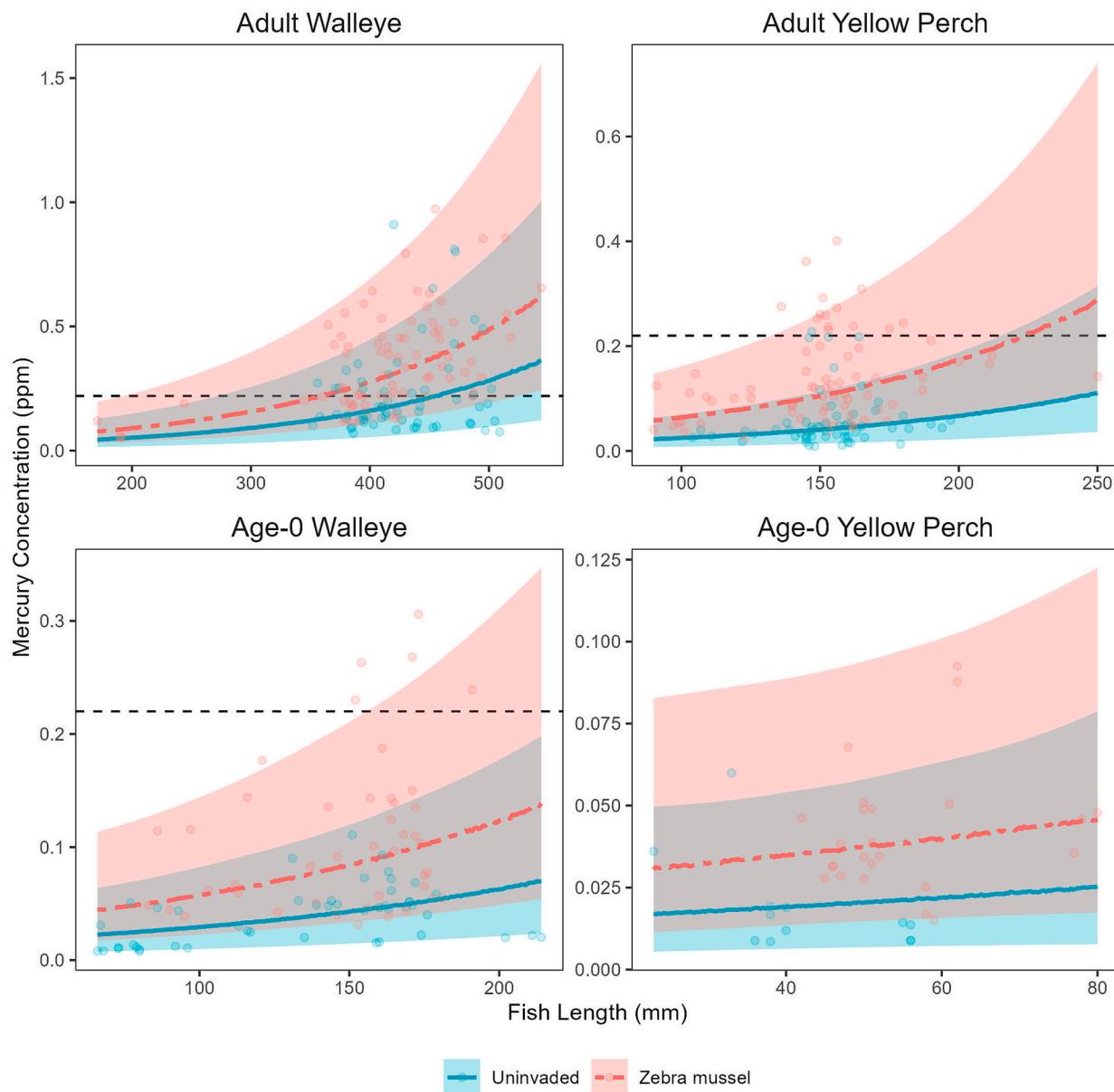
### 3.3. Lake condition and water chemistry

On average, lakes containing zebra mussels were similar in lake and watershed characteristics to uninvaded lakes (Table S11). The only exceptions were that lakes containing zebra mussels were larger in surface and littoral areas (but not proportion littoral) than uninvaded lakes (Wilcoxon *p*-values <0.05; Table S11, Fig. S6). Measured DOC did not differ between uninvaded ( $6.26 \pm 2.11$  mg/L) and invaded lakes ( $6.30 \pm 1.73$  mg/L). Similarly, filtered total mercury within lake water was similar between uninvaded ( $0.21 \pm 0.09$  ng/L) and zebra mussel invaded lakes ( $0.23 \pm 0.07$  ng/L). Furthermore, filtered methylmercury in surface waters was only above method detection limit (0.04 ng/L) at

two sites, one uninvaded lake (Lake Koronis) and one lake with zebra mussels (Chippewa Lake; Table S1).

### 4. Discussion

Aquatic invasive species can profoundly alter ecosystems, including alterations to contaminant cycling and bioaccumulation (Eagles-Smith et al., 2018; DeRoy and MacIsaac, 2020). Considering the importance of walleye and yellow perch as a food resource for Indigenous communities and recreational anglers, it is critical to understand how perturbations such as species invasions influence methylmercury in fish consumed by humans. Here, we demonstrate that mercury concentrations in walleye

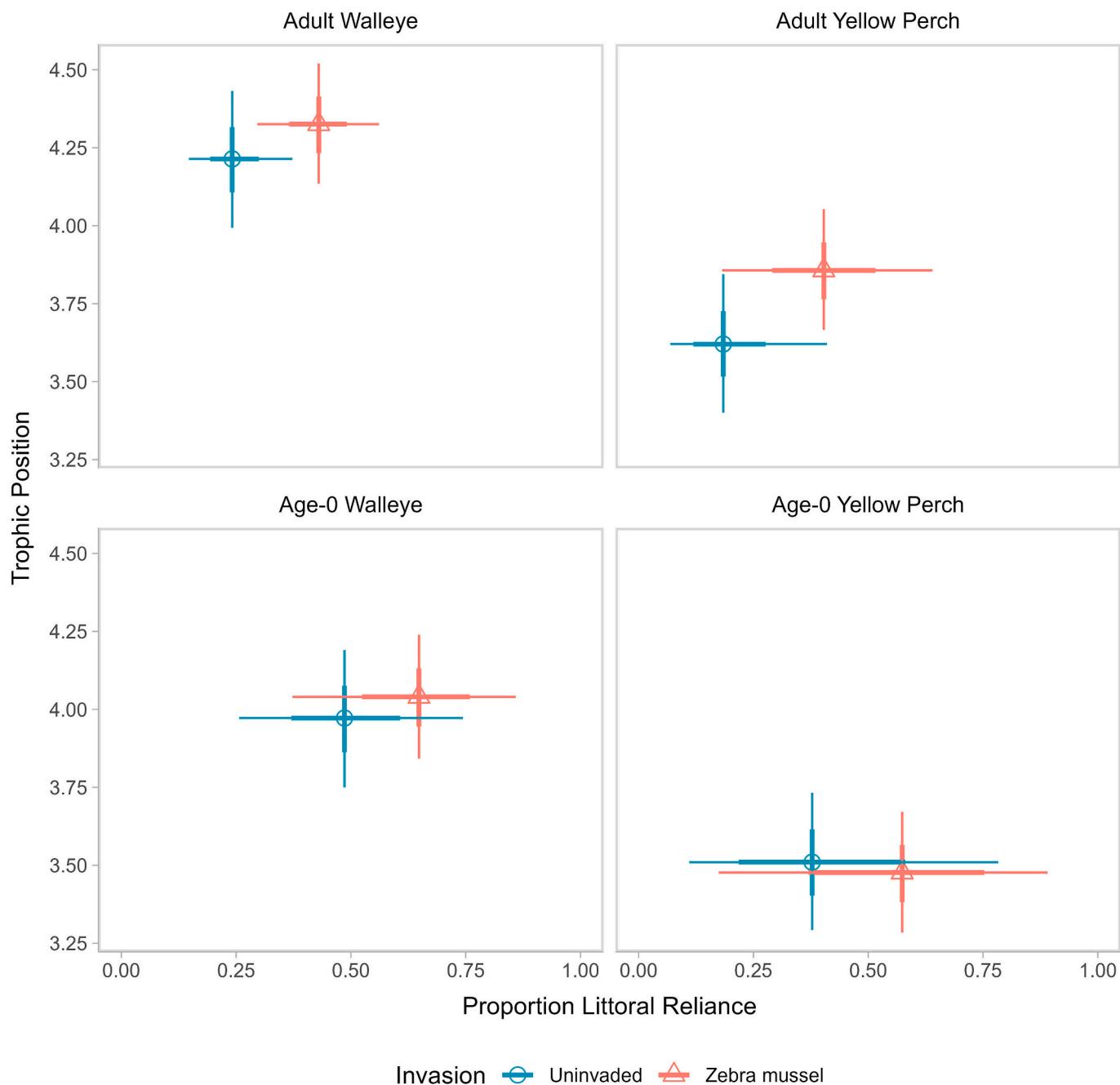


**Fig. 3.** Predicted mercury concentrations (in ppm wet weight) as a function of fish total length for adult and age-0 walleye and yellow perch in lakes invaded by zebra mussels and uninvaded lakes (assuming average conditions of other lake characteristics, and averaged across lake connectivity class). Median concentrations are represented by lines and 95 % credible intervals are represented by transparent ribbons. Points are observed values. The horizontal dotted lines at 0.22 ppm represent the Minnesota Department of Health threshold that warrants reducing the frequency of fish consumption from one meal/week to one meal/month for sensitive groups (Great Lakes Consortium, 2007).

and yellow perch tissues were higher in lakes containing zebra mussels compared to uninvaded lakes, and these differences were concurrent with differences in fish resource use. Mercury concentrations in adult walleye were more than twice as likely to be over 0.22 ppm, the fish tissue mercury concentration threshold triggering more stringent consumption guidance for sensitive populations (children and women of childbearing age) from one meal per week (0.11–0.22 ppm) to one meal per month (0.22–0.95 ppm Hg) (Great Lakes Consortium, 2007). Furthermore, walleye and yellow perch are predicted to exceed the 0.22 ppm threshold at smaller sizes in lakes containing zebra mussels. As of March 2024, at least 16 % of Minnesota lakes managed for walleye were designated as invaded with zebra mussels (Minnesota Department of Natural Resources, 2024), and an increasing number of those lakes are in reservations and treaty-ceded territories where tribal fishing rights are maintained with walleye as a target species. Walleye harvest is frequently managed by minimum length limits (e.g., Fayram et al.,

2001; Isermann, 2007), and harvest and consumption of walleye and yellow perch frequently targets fish equal to or greater than the lengths at which they are predicted to exceed critical mercury levels in invaded lakes (e.g., Lynch et al., 2021). Thus, zebra mussel invasion may result in a greater potential mercury consumption risk to humans.

Mercury in fish tissues is controlled by multiple factors, and we hypothesize that zebra mussels affect mercury concentrations in fish via several pathways (Eagles-Smith et al., 2018). First, similar to previous observations for dreissenids and associated *Cladophora* mats in Lake Michigan (Lepak et al., 2015), zebra mussel accumulations in the littoral zone give rise to substantially reduced redox status of littoral sediments and thereby promote biogeochemical conditions more favorable for obligate anaerobic microbial communities capable of methylating inorganic mercury. Through this pathway, zebra mussels may increase methylmercury bioavailability and/or concentrations in littoral zone, including sediments, porewater, benthic infauna, and biota foraging in



**Fig. 4.** Littoral reliance and trophic position for adult and age-0 walleye and yellow perch in lakes invaded by zebra mussels and uninvaded lakes. Proportions were estimated for fish of mean total length for each group (adult walleye 420 mm or 16.5 in; adult yellow perch 151 mm or 6.0 in; age-0 walleye 142 mm or 5.6 in; age-0 yellow perch 51 mm or 2.0 in). Dots represent medians; heavy lines represent 66 % credible intervals, and thin lines represent the 95 % credible interval of posterior estimates for each group.

this environment. Walleye and yellow perch in our study lakes relied more on littoral energy sources in zebra mussel-invaded lakes compared to uninvaded lakes, consistent with hypothesized food web alterations that can lead to increased contaminants in fish by concentrating consumption in areas where mercury methylation is occurring (Eagles-Smith et al., 2008; Azim et al., 2011; Lepak et al., 2019). However, littoral reliance varied substantially among lakes, suggesting that the overall effect of zebra mussels on fish tissue mercury operates on multiple pathways that we cannot completely describe with this study. In addition to potential influences on methylation rates and food webs, increased water clarity due to zebra mussel invasion can reduce methylmercury in the photic zone via photo demethylation (Seller et al., 1996; Krabbenhoft et al., 1998; Black et al., 2012) while simultaneously

reducing walleye habitat and biomass production (Geisler et al., 2016; Lester et al., 2004; Mahlum et al., 2023). Habitat changes associated with zebra mussels can lead to slower growth rates of walleye and yellow perch at both adult and age-0 life stages (Nienhuis et al., 2014; Hansen et al., 2020), which would be expected to increase mercury concentrations as slower growing fish are older for a given length and thus have had more time to bioaccumulate mercury in their tissues (Simoneau et al., 2005; Johnston et al., 2022). Future research partitioning the effects of each of these pathways would help identify potential strategies for reducing mercury exposure.

This study is the first to document increased mercury concentrations in fish tissues associated with zebra mussel invasion in inland lakes across multiple trophic levels and life stages. The combined results of

increased mercury in fish tissues and increased littoral reliance of fish in invaded lakes is consistent with the processes observed in piscivorous fish in Lake Michigan (Lepak et al., 2019). Still, higher fish tissue mercury in lakes containing zebra mussels could potentially be due to other factors affecting mercury delivery or methylation between the lake groups, and we observed variability among lakes and uncertainty in our estimates of the effect of zebra mussels. We attempted to control for potential confounding variables by selecting lakes from each invasion status (invaded and unininvaded) from the same region and with similar characteristics, although we cannot causally rule out other factors. Measured total mercury and methylmercury in the water column did not differ between invaded and unininvaded lakes, indicating no obvious differences in mercury loading or cycling among invaded and unininvaded lakes. DOC is a known driver of methylmercury production in aquatic ecosystems (e.g., Moreau et al., 2015; Peterson et al., 2023); however, DOC did not differ between unininvaded and zebra mussel invaded lakes. Similarly, the percentage of wetlands in the watershed is positively correlated with fish tissue mercury (e.g., Rypel, 2010) but neither total wetland area nor percent wetlands differed between invaded and unininvaded lakes. Invaded lakes were on average larger in surface area and volume, and previous research reported negative relationships between fish tissue mercury and lake size (e.g., Bodaly et al., 1993; Rasmussen et al., 2007; Rypel, 2010), suggesting larger lake area would be expected to result in lower fish tissue mercury concentrations in lakes containing zebra mussels, rather than the higher concentrations reported here. Similarly, watershed to lake area ratios of unininvaded lakes were somewhat higher than those of invaded lakes (though not statistically significant), which would be expected to correlate with higher mercury flux in unininvaded lakes (e.g., Hutcheson et al., 2008; but see Sumner et al., 2020), counter to our observations. The inclusion of these variables in a statistical model did not explain variation in fish tissue mercury nor meaningfully affect the estimated effect of zebra mussels (Tables S7 and S10), strengthening our hypothesis that zebra mussels are a causative agent in fish tissue mercury.

Changes to aquatic food webs and mercury bioaccumulation associated with zebra mussel invasion have potential implications for the fish populations themselves. Even low levels of methylmercury reduce growth and gonadal development in walleye (Friedmann et al., 1996). Increased littoral reliance could be interpreted as a sign of percid resilience to zebra mussel invasions, as these species adapt to increased littoral habitat area and secondary production resulting from the establishment of zebra mussels. However, the higher reliance on littoral resources in invaded lakes could result in changes to walleye and yellow perch populations and community dynamics. Large-scale, multiple-lake studies in Canada reported walleye biomass declines associated with zebra mussel invasion (Nienhuis et al., 2014; Gutowsky et al., 2019). In Minnesota's largest lakes, young-of-year walleye grew more slowly in lakes invaded by zebra mussels (Hansen et al., 2020), though there were no consistent patterns of increased littoral resource use by percids in those same large lakes (Bethke et al., 2023). Our results suggest that the capacity to use littoral resources following zebra mussel invasion may have consequences for toxin accumulation in fish tissues, and the ultimate impacts on fish populations and communities is an important area of future research.

Increased mercury concentrations in percids adds to a growing list of negative effects of invasive zebra mussels and highlights how ecological stressors can alter contaminant cycling within inland lakes. To manage methylmercury exposure risk, agencies monitor and provide both general and waterbody-specific guidance for fish consumption, and regional tribal authorities have developed culturally specific mercury reduction frameworks to encourage safe fish harvest and consumption practices (Madsen et al., 2008; DeWeese et al., 2009; Foran et al., 2010; Orgon, 2022). Although many state, provincial, and tribal government agencies monitor mercury in fishes regularly (e.g., Rasmussen et al., 2007; Monson, 2009; Foran et al., 2010), monitoring programs were not designed to detect the effects of species invasions on mercury

bioaccumulation against a background of variability in deposition, methylation, and food web configurations that lead to variable fish tissue mercury concentrations. Given the results of our study, additional monitoring of mercury concentrations in fish may be needed in zebra mussel-invaded lakes to further elucidate long-term trends and drivers of bioaccumulation.

## CRediT authorship contribution statement

**Naomi S. Blinick:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Formal analysis. **Denver Link:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Tyler D. Ahrenstorff:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Bethany J. Bethke:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Abram B. Fleishman:** Writing – review & editing, Resources, Formal analysis. **Sarah E. Janssen:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David P. Krabbenhoft:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Jenna K.R. Nelson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation. **Heidi M. Rantala:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Claire L. Rude:** Writing – review & editing, Methodology, Investigation. **Gretchen J.A. Hansen:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gretchen Hansen reports financial support was provided by Minnesota Environment and Natural Resources Trust Fund as recommended by the Minnesota Aquatic Invasive Species Research Center (MAISRC) and the Legislative-Citizen Commission on Minnesota Resources (LCCMR). Gretchen Hansen reports financial support was provided by the U.S. Geological Survey (USGS) in cooperation with the National Institutes for Water Resources. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.177515>.

## Data availability

Data and code are available in: Blinick, NS; Ahrenstorff, TD; Bethke, BJ; Fleishman, AB; Link, D; Nelson, JKR; Rantala, HM; Rude, CL; Hansen, GJA. (2023). Data and R code for analysis of mercury concentration and food web differences in walleye and yellow perch from Minnesota lakes with and without invasive zebra mussels, 2019 - 2021. Data Repository for the University of Minnesota, <https://doi.org/10.13020/xb7g-yc85>. All mercury data are available in Tate, M. T., Janssen, S.E., Blinick, N., Link, D., Nelson, J.K.R., Hansen, G., and Krabbenhoft, D.P., 2024, Walleye (*Sander vitreus*), Yellow Perch (*Perca flavescens*) and Surface Water Mercury Concentrations in Minnesota Lakes: U.S. Geological Survey data release, <https://doi.org/10.5066/P9XGZD51>.

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